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Abiotic barriers limit tree invasion but do not hamper native shrub recruitment in invaded stands

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Abstract The interplay between the invasion of alien plant species and re-colonization of native plant species is important for conservation. Sandy coastal plains (called *restinga* in Brazil) were used as a model system to explore the abiotic barriers that potentially limit the initial establishment of alien and native woody plants in invaded and non-invaded areas. The study tested the influence of light availability, soil type and litter layer on recruitment of a wind-dispersed alien tree (*Casuarina equisetifolia*) and two bird-dispersed native shrubs under a *Casuarina* stand and in the preserved restinga. The effect of soil type and the physical and allelopathic effects of *Casuarina* litter on seedling emergence of the three species were also evaluated under greenhouse conditions. Low dispersal associated with low seedling emergence and zero survival of young plants (mainly due to microhabitat conditions) apparently prevents the spread of *Casuarina* in the preserved restinga. The main cause of low recruitment of native species in the *Casuarina* stand was the physical barrier of the litter. However, if seeds overcome this physical barrier, the presence of litter improves seedling emergence and survival of young plants, mainly because the litter increases soil moisture. Sowing seeds below litter and planting young plants of native shrubs on litter can improve the re-colonization of native plants in invaded areas. In conclusion, *Casuarina* invasion on sandy coastal plains is strongly limited by abiotic barriers, but anthropogenic disturbances are altering the key processes that naturally make the restinga resistant to invasion.

Keywords *Casuarina equisetifolia* · Litter · Seed dispersal · Seedling emergence · Restinga · Tree invasion

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Introduction

Abiotic and biotic barriers often limit the establishment success of alien plants in their new environment (Lonsdale 1999; Levine et al. 2004). On the other hand, invasive plant species modify interspecific interactions and alter ecosystem functions in the new habitat (Hulme 2007; Vilà et al. 2011), creating "novel ecosystems" (i.e. ecosystems that have been irreversibly altered, but which can provide ecological

values that need to be preserved; Hobbs et al. 2014). Recruitment of native species is often impeded in such ecosystems (Ens and French 2008; de la Penã et al. 2010; Novoa et al. 2012). Although both are important for conservation of the ecosystems, little attention has been given to the concomitant interplay between invasion of alien plant species and native plant re-colonization (Emer and Fonseca 2011; Fuentes-Ramírez et al. 2011).

Traits related to reproduction and dispersal are crucial for allowing alien species to overcome a series of barriers to become naturalized or invasive (Blackburn et al. 2011; Richardson and Pyšek 2012). Even if seed dispersal occurs, alien species can only invade if seeds (or other propagules) reach suitable habitat, germinate, and establish (Coutts et al. 2011). Knowledge of the factors that mediate seed germination, seedling survival and growth is therefore essential for determining potential areas of invasion (McAlpine and Jesson 2008; Dechoum et al. 2015). Nonetheless, seed and establishment limitation are usually investigated separately (Warren et al. 2012), which hampers our ability to understand interactions between these potential barriers or opportunities in the invasion process.

When an alien species invades a new habitat, it often modifies abiotic factors, reducing regeneration rates of native species (Ens and French 2008; Hata et al. 2010a; Loydi et al. 2015). Invasive tree species can limit light availability, which may hamper the recruitment and growth of native shade-intolerant species (Fuentes-Ramírez et al. 2011). The moisture content of the soil can be reduced by invasive species, preventing germination of the native vegetation (Novoa et al. 2014). Some alien species can also release allelopathic substances and affect the chemicals of the soil, which may limit the establishment of native species (Bais et al. 2003; Inderjit et al. 2008). Plant litter is another key factor in the recruitment, and may have positive (by decreasing the amplitude of fluctuations in soil temperature and evaporation; Eckstein and Donath 2005; Hovstad and Ohlson 2008) or negative effects (by creating physical and/or chemical barriers—the former generally stronger the latter; Rotundo and Aguiar 2005; Hovstad and Ohlson 2008) during the early life-cycle stages of the plants (Facelli and Pickett 1991; Xiong and Nilsson 1999). Although invasive species can alter abiotic factors, such as light availability, soil factors, and features of the litter layer, some native species have the capacity to re-colonize invaded areas (Guerrero and Bustamante 2007; Fuentes-Ramírez et al. 2011; Hata et al. 2012). As the removal of an invasive species is usually difficult and expensive (Pimentel et al. 2000; van Wilgen et al. 2016), a better understanding of the factors that limit establishment of native species is required to implement effective recovery efforts in areas affected by invasive species (Ens and French 2008; Fuentes-Ramírez et al. 2011). However, little is known about the potential for re-colonization of native plant species in invaded stands (Holmes and Richardson 1999; Emer and Fonseca 2011; Fuentes-Ramírez et al. 2011), especially in stressful environments.

Sandy coastal plains are ecosystems with multiple stressful conditions (e.g. high solar radiation, drought, high temperatures and salinity, burial; Reinert et al. 1997; Hesp and Martínez 2007), which can limit germination and establishment of plants (Scarano 2009). A type of vegetation called *restinga* (sensu Araújo 1992) occurs in sandy plains along the Brazilian coast, extending from the Equator to below the Tropic of Capricorn—a distance of about 3.900 km (Lacerda et al. 1993). Some restingas have a patchy structure and are denominated as open scrub vegetation. Extensive areas of sandy coastal plains around the world are covered by open scrub vegetation that may lie behind the coastal thicket or farther inland (Araújo and Pereira 2002). Open scrub vegetation presents two distinct microsites: patches (supporting high species diversity and abundance) and open areas (usually covered by low herbaceous species diversity) (Araújo and Pereira 2002; Correia et al. 2010). Patches have greater water availability and lower irradiance and temperature than open areas (Pugnaire et al. 2004; Gómez-Aparicio et al. 2005). However, shady conditions inside patches can have negative effects on plant recruitment by reducing photosynthesis rates (Callaway and Walker 1997; Hastwell and Facelli 2003). The restinga supports several rare, endemic and threatened species (Araújo and Pereira 2002; Rocha et al. 2007; Scarano 2009). This ecosystem is subject to high levels of degradation (Araújo and Pereira 2002; Rocha et al. 2007), mainly through vegetation removal for housing development and the establishment of alien plant species, such as *Casuarina equisetifolia* L. (Rocha et al. 2007).

Casuarina equisetifolia is one of the world's most widespread invasive alien tree species (Rejmánek and

Richardson 2013). It is native to the east coast of Australia and Southeast Asia and it has been planted in coastal regions in many parts of the world (Morton 1980; Parrotta 1993; Potgieter et al. 2014). *Casuarina equisetifolia* was introduced to Brazil mainly after 1950, when it was widely planted along the coast in the restingas (I3 N Brazil 2016). The species is now naturalized in many parts of the country (Zenni and Ziller 2011; Potgieter et al. 2014). Given the widespread planting and the large extent of climatically suitable areas in the country, there is a large invasion debt (sensu Rouget et al. 2016); further naturalizations and invasions are inevitable in the future. Little recruitment of native species occurs under *Casuarina* stands, which may be due to the lack of seed dispersal (Hata et al. 2009) and/or inhibition of germination and seedling establishment due to the thick litter accumulation of this tree (Parrotta 1995, 1999; Hata et al. 2009, 2010a, b). However, the main causes of low natural regeneration in areas invaded by this alien species on sandy coastal plains are not known. The invasion of *C. Equisetifolia* in the Brazilian restingas thus provides a good model system to explore the environmental factors that limit the invasion of an alien species and the potential for re-colonization of native plants in invaded areas, considering both seed dispersal to the survival of young plants.

We assessed the influence of three environmental factors expected to be key determinants of early seedling recruitment: light availability, soil type and litter layer. We evaluated: (1) seed dispersal, (2) seedling emergence and seedling establishment, (3) young plants survival and growth of an alien tree (*C. Equisetifolia*) and two native shrubs (*Clusia hilariana* and *Maytenus obtusifolia*) in an invasive stand of *Casuarina* and inside vegetation patches in the restinga, using experimental manipulations of litter. In open areas of the restinga, we only sown seeds and planted young plants of *C. Equisetifolia,* because it is known that regeneration of *C. hilariana* and *M. obtusifolia* is restricted to sites inside patches (Matos 2014). We also undertook a greenhouse experiment to assess how differences in soil type and physical and allelopathic properties of litter affected seedling emergence for the three species. The following hypotheses were examined: (1) *C. equisetifolia* exhibits higher levels of seed dispersal, emergence, survival and growth capacity under its own canopy than in preserved restinga; (2) seed dispersal and recruitment by native shrubs are only successful inside vegetation patches; (3) soil under *Casuarina* stand has chemical substances that limit the establishment of native species; (4) the litter layer of *C. equisetifolia* decreases rates of recruitment of native plants, and (5) the physical effects of *Casuarina* litter are stronger than its chemical effects.

Materials and methods

Study species

Casuarina equisetifolia L. (Casuarinaceae) (Australian pine or coastal she-oak) is a fast-growing, evergreen tree that attains a height of 10–40 m. The species is wind-pollinated and reproduction is mainly by seeds (Morton 1980; Apfelbaum et al. 1983), but it can also propagate vegetatively (Rentería 2007). Seeds consist mostly of a membranous samara, have dry mass of 0.001 g (Zimmermann et al. 2016), and are enclosed within a nut borne in a 4–5 mm long cone (Whistler and Elevitch 2006). Large numbers of seeds are produced (Apfelbaum et al. 1983) and dispersal is mainly by wind (Morton 1980) but also by water (Rentería 2007), although we could find no information on dispersal distances. The species forms a permanent seed bank, with a predicted seed viability of 50 months (Zimmermann et al. 2016).

Clusia hilariana Schltdl. (Clusiaceae), a shade-tolerant evergreen native shrub (Matos 2014), occurs along the southeastern and northeastern Brazilian Atlantic Forest (Bittrich et al. 2015). The species can attain 8 m high, and it is an important component of some woody vegetation patches in the restingas. This shrub is a key nurse plant, providing safe germination sites for other plant species (Scarano 2002; Dias et al. 2006). It is a dioecious species and fruit production occurs between January and May (Faria et al. 2006). Fruits are globular capsules that are rich in lipids (Barroso et al. 1999). Seeds have a dry mass of 0.05 g (Matos 2014), a thin coat (Braz and de Mattos 2010), an orange aril (Cavalcante et al. 2010) and are dispersed by birds (Gomes 2006). The species has obligate CAM-photosynthesis (Franco et al. 1996) which may favor seedling survival during periods of water shortage (Cavalcante et al. 2010).

Maytenus obtusifolia Mart. (Celastraceae), a shade-tolerant (Matos 2014) evergreen native shrub that

seldom grows taller than 5 m (Benevides et al. 2013), occurs in several states of northeastern and southeastern Brazil (Lombardi et al. 2015). In the restinga of the Costa do Sol State Park it is one of the most common species in the patchy shrub vegetation (Araújo et al. 2009). Individuals can be dioecious or hermaphrodites (Benevides et al. 2013). Fruit production is mostly between January and April (T.G. Zimmermann, per. obs.). The fruit is a capsule that is red when ripe and opens into two valves; it contains 1–3 seeds surrounded by a white pulp. Seeds have a dry mass of 0.06 g (Matos 2014) and are dispersed by birds.

Study area

The study site is located in the restinga of the Costa do Sol State Park (22° 58′S, 42° 01′W, sea level), in Arraial do Cabo, state of Rio de Janeiro, Brazil. The PECSol sandy plains occur between the Atlantic Ocean and the Araruama lagoon, the largest hypersaline lagoon in the world. This region is characterized by a hot, semiarid climate, with 800 mm of annual precipitation, occurring predominantly during summer (November to February) (Barbiére 1984). Annual precipitation in 2014 and 2015 in Arraial do Cabo was 718 and 577 mm, respectively, with minimal rainfall in January 2015 (0.2 mm) and maximum rainfall in April 2014 (193 mm) (Figure S1, in the Supporting Information). Periods of low soil water potential are very common in the restinga throughout the year, due to low capacity of the sandy soil to retain water and the occurrence of dry spells during rainy season (Cavalin and de Mattos 2007). Mean annual temperature in the restinga of the PECSol is 25 °C, with minimum and maximum temperatures of 12° and 36 °C, respectively (Scarano 2002).

Most individuals of *C. equisetifolia* in the restinga of the PECSol were planted close to Araruama Lagoon. Naturalized populations of the species are mainly close to this lagoon, in degraded areas and in abandoned salines. The study area is 25.1 ha in extent and has one of the largest *Casuarina* stands (2.2 ha) adjoining an uninvaded restinga (22.9 ha) in the park. The *C. equisetifolia* stand has 0.31 individuals m^{-2} (3.048 ind ha^{-1}), height of 7.27 m ± 3.86 m and diameter at breast height of 5.77 ± 5.18 cm (n = 450). Data on photosynthetic photon-flux density (PPFD %) and red/far-red light ratio (R:FR; mol mol^{-1}) in the *Casuarina* stand were measured at 20 points separated by 20 m. Values of PPFD % were 68.5 ± 11.2 % and R:FR were 1.05 ± 0.10 mol mol^{-1}. Inside patches values of PPFD % were 1.7 ± 0.6 % and R:FR were 0.29 ± 0.05 mol mol^{-1} (Matos 2014). Values of PPFD % were calculated by taking as reference the mean full sunlight (100 % PPFD = 2305.3 µmol m^{-2} s^{-1}). All measurements were made at midday, on sunny cloud-free days with a radiometer SKR-100 linked to a SpectroSense 2 SKL 904 (Skye Instruments, Llandrindod Wells, UK).

Seed collection and seed viability

Seeds of *C. equisetifolia* and the two native species were collected between February and March 2013 from at least 10 plants per species. Minimum distance between selected seed trees was 10 m. Seeds were removed from the fruit in the laboratory and then stored in sealed plastic bags at 10 °C. Initial seed viability was determined by placing six replicates of 50 seeds on two moist filter papers in Gerbox. Seeds were incubated in a germination chamber at 25 °C (*C. hilariana* and *M. obtusifolia*) or 30 °C (*C. equisetifolia*), at 8/16 h photoperiod. Germination was recorded and distilled water was added every three days. Final germination was 74.2 ± 7.4 % for *C. equisetifolia*, 80.8 ± 8.8 % for *C. hilariana* and 88.4 ± 7.6 % for *M. obtusifolia*.

Field experiments

Experiments were conducted to evaluate (1) seed dispersal, (2) seedling emergence and seedling establishment, (3) young plant survival and growth for the three species in an area invaded by *Casuarina* and in vegetation patches in the restinga. For *C. equisetifolia* seeds were also sown and young plants were planted in open areas in the restinga (Table 1).

Seed dispersal

Twenty seed traps were placed in each vegetation type to estimate annual seed dispersal. Beneath *Casuarina* canopies the traps were set 20 m apart and inside patches they were separated by 50 m. The difference in the distance between seed traps for each vegetation type was due to the different size of each environment (*Casuarina* stand = 2.2 ha; restinga = 22.9 ha). Seed traps were made from two wooded stakes of 0.5 m

Table 1 Description of experimental treatments (field and greenhouse) and experimental design. Study species were an alien species (*Casuarina equisetifolia*) and two native species (*Clusia hilariana* and *Maytenus obtusifolia*)

Experimental treatments	Conditions	Experimental design	Area of each repetition	Assesment
Field				
Seed dispersal		20 seed traps	0.5 m^2	Once per month—Annual
Seedling	Above, below and without litter	6 × 50 seeds	0.04 m^2	
Emergence				Once per month—4 months
Establishment				Once per month—24 months
Young plant	With and without litter	6 × 5 young plants	3 m^2	
Survival				Once per month—24 months
Growth				Once per year—2 years
Greenhouse				
Soil	Patches, *Casuarina* stand, sterilized *Casuarina* stand	5 × 25 seeds	0.02 m^2	Once per week—12 weeks
Litter	Below litter, below plastic fibers, above litter	5 × 25 seeds	0.02 m^2	Once per week—12 weeks

Field experiments were conducted in the restinga of the Costa do Sol State Park (Brazil) under three conditions: *Casuarina* stand, vegetation patches and open areas (only for *C. equisetifolia*). Greenhouse experiments were conducted in the Botanical Garden of Rio de Janeiro

long, joined by a metal clamp with a diameter of 0.8 m and surface area of 0.5 m^2. A white cloth with 0.1 mm mesh was fixed inside the seed trap using an elastic band at the metal clamp. The two vegetation types were visited once a month between April 2013 and March 2014. During each visit, cloths were collected and replaced. The collected seeds of the alien species and the two native plants were separated and counted in the laboratory.

Seedling emergence and establishment

To avoid seed-size effect, the larger and smaller seeds were removed and those with median size were chosen. To separate the seeds of *C. equisetifolia* a seed blower was used. Six plots of 2 × 2 m were established in each vegetation type. In *Casuarina* stand the minimum distance between plots was 20 m. In the restinga, each plot was located inside a patch with *C. hilariana* as a dominant species, with a minimum distance of 50 m between patches. Minimum size of patches was 6 × 6 m. Three parallel transects were laid out in each plot and seeds of one species were sown in each transect. For each transect three 0.2 × 0.2 m subplots (hereafter the seed subplots) were established, separated by 0.2 m. Each seed sub-plot was surrounded with 1 mm^2 pore screen mesh, fixed with four metal wires to prevent seed predation by animals and seed removal by wind. To evaluate effects of litter on seedling emergence, each seed subplot was subjected to a different treatment of seed sowing: *(i)* above, *(ii)* below and *(iii)* without litter layer. Fifty seeds of each species were sown in each seed subplot (50 seeds × 3 seed subplot × 6 plots = 900 seeds/species/vegetation type). The depth of the litter layer was 4 cm. The mean litter depth was measured at 20 random points (Mean = 4.53 ± 2.20 cm). As controls, we established two seed subplots (0.2 × 0.2 m), with and without litter. These were needed to verify the contribution of the seed bank to seedling emergence. These were not included in analyses as they were only used to assess potential site and treatment contamination. In the open area we sowed only *C. equisetifolia* seeds without litter. After sowing, each seed subplot was irrigated with 200 ml of water. Sowing seeds were carried out in March 2014, following natural seed dispersal events for the three species. Seedling emergence was defined by shoot emergence. Emergence was recorded monthly as the number of seedlings appearing in the first four months (until July 2014), when emergence had ceased. Seedling emergence proportion P(Em) was defined as the total number of emerged seedlings divided by the total number of seeds initially disposed in each seed

subplot (i.e. 50 seeds). Seedling establishment proportion P(Es) was defined as the total number of seedlings that survived after 24 months of sowing (February 2016) divided by the total number of emerged seedlings (Guerrero and Bustamante 2007).

Recruitment expectancies for each species were calculated based on seed dispersal, emergence and establishment (Vilà and Lloret 2000) in each vegetation type (*Casuarina* stand and inside vegetation patches) under three different conditions (above, below and without litter). Emergence was estimated by the number of seeds dispersed multiplied by the P(Em) and establishment was estimated by the emergence multiplied by the P(Es).

Young plant survival and growth

Between March and April 2013 seeds were incubated in a germination chamber at 25 °C (*C. hilariana* and *M. obtusifolia*) or 30 °C (*C. equisetifolia*) at 8/16 h photoperiod. In May 2013 seedlings were transferred to the greenhouse of the Rio de Janeiro Botanical Garden. One month before seedlings were transplanted to the field, the irrigation was reduced for acclimatization. Before the transplant, young plants were measured and the larger and smaller ones were removed to ensure similar sizes within species. The average plant height was 12.58 ± 2.05 cm for *C. equisetifolia*, 9.42 ± 2.06 cm for *C. hilariana* and 11.57 ± 1.31 cm for *M. obtusifolia,* and the average number of leaves was 9.02 ± 2.14 for *C. hilariana* and 12.33 ± 1.48 for *M. obtusifolia.* In December 2013, young plants were transplanted to the field. Six plots (4 m x 3 m) were established in each vegetation type. The minimum distance between plots in the *Casuarina* stand was 20 m. In the restinga, plots were inside the same patches as were used for sowing seeds. Inside each plot, six parallel transects, separated by 0.5 m, were established. Thirty young plants were planted in each plot, 10 of each species—five young plants of one species along each transect. To evaluate the effects of litter removal on the survival and growth of young plants, half of the plants were planted with and half without litter layer (4 cm thick). Sixty young plants of each species were planted in each vegetation type. Only young plants of *C. equisetifolia* ($n = 30$) were planted in open areas, without litter. A total of 390 young plants were planted (30 young plants × 3 species × 2 conditions of litter × 2 vegetation types + 30 young plants of *C. equisetifolia* in the open area = 390). Young plants were separated by 50 cm to avoid direct effects of competition. All plants were labeled on the day of planting. After planting, each young plant was irrigated with 100 ml of water. The survival of young plants was monitored monthly over 15 months and the final evaluation was done after 24 months (December 2015). At the beginning of the experiment, the end of the 1 year (December 2014) and the end of the 2 year (December 2015) the height and total number of leaves of each living young plant was noted. The number of leaves was not counted for *C. equisetifolia* as the leaves are too small to be easily counted.

Greenhouse experiments

To evaluate the effects of soil type and physical and allelopathic properties of litter on emergence of seedlings of the three species, experiments were conducted in the greenhouse of the Rio de Janeiro Botanical Garden, between March and June 2013 (Table 1).

Soil samples and litter were collected in March 2013. Soil samples were collected in the *Casuarina* stand and inside vegetation patches in the restinga. In the *Casuarina* stand six random sites (0.5 × 0.5 m) were selected near a *C. equisetifolia* individual to collect sandy soil. In the restinga, soil samples were taken from sites (0.5 × 0.5 m) inside the patches where seeds had been sown and young plants planted. Litter was removed prior to soil collection. Soil samples were taken from the top 10 cm at each point. Half the amount of soil collected in the *Casuarina* stand was sterilized by autoclaving (1.0 KgF cm^{-2} and 120 °C) to remove any secondary metabolites. In the greenhouse, seeds were sown under three conditions: (1) *Casuarina* stand soil, (2) sterilized *Casuarina* stand soil, and (3) soil from patches. Seeds were buried at a depth of 2 cm in the soil.

Casuarina equisetifolia litter was also collected at six random points. Litter was mixed and air dried before the experiment. To test the physical effect of litter, seeds were buried in vermiculite and covered with litter (below-litter treatment) or placed above the litter layer (above-litter treatment). To determine the chemical effect of litter, seeds were buried in vermiculite and covered by plastic fibers (below plastic fiber treatment). Plastic fibers were of similar size and shape

to *C. equisetifolia* litter. As plastic does not produce allelopathic compounds (cf. Facelli and Picket 1991), release of allelopathic substances from litter would decrease emergence under litter in relation to plastic fibers, being attributable to a chemical effect. However, if negative effects on seedling emergence occur in both litter and plastic fibers, these would be attributable to a physical effect. The thickness of litter layer and plastic fibers applied was 4 cm (60 g 0.02 m^{-2} for litter and 54 g 0.02 m^{-2} for plastic fibers). As control, seeds were buried in vermiculite.

Treatments consisted of 25 seeds of each species sown in 2-L pots (0.02 m^2, with 16 cm in length x 12 cm in width x 10.5 cm in height), arranged in five blocks (replicates). Treatments were assigned randomly to pots within each block (randomized block design). Each pot was filled with 4 cm (750 ml) of soil or vermiculite. Experimental pots were watered once or twice a week. Substrate moisture was monitored weekly from three soil samples per treatment, as gravimetric moisture content (103 °C for 24 h). Seedling emergence (shoot emergence) was recorded every week for 3 months, when emergence had ceased.

Data analysis

To test differences between seed dispersal of the three species in relation to vegetation type (*Casuarina* stand and vegetation patches) we used the Mann–Whitney U test, as the Shapiro–Wilk test revealed that the data did not conform to expectations of normality.

Generalized linear mixed models (GLMM) for nested data were used to evaluate the seedling emergence and establishment in the field. The response variable was the proportion of seedling emergence after four months and seedling establishment after 24 months. The Binomial distribution was assumed for the response variable and the logit function for the relationship between the response and explanatory variables. The explanatory variables vegetation type (*Casuarina* stand and patches), seed sowing position (above, below and without litter), and the interaction between these factors were initially considered fixed effects. As the variables were highly correlated, the inclusion or exclusion of fixed effects for each species was based on Akaike Information Criterion values calculated using maximum likelihood. Seed subplots were spatially dependent, whereas plots were considered replicates of each vegetation type and inserted into the model as a random effect. The GLMMs were performed with random intercepts and slopes. The mixed model was fitted using maximum likelihood and adaptive Gauss–Hermite quadrature to the deviance.

To assess the survival of young plants, the Kaplan–Meier product limit method was used to estimate the survival function, and a Log-rank test was used to test for significant differences in survival curves among treatments. Cox regression was used to evaluate the effects of vegetation type, presence of litter and their interactions on probability of the death of young plants.

The annual growth of young plants was assessed by examining the difference in height and number of leaves at the end of the first year compared to the beginning of the experiment (Δheight or number of leaves year one = time 12 months—time 0 month), and at the end of the second year compared to the end of the first year (Δheight or number of leaves year two = time 24 months—time 12 months) for each surveyed young plant. Generalized linear models (GLM) were used to evaluate differences in the growth in the first (2014) and in the 2 year (2015) between the treatments. The response variable was the height increment and the increase of the number of leaves per year. The explanatory variables vegetation type (*Casuarina* stand and patches) and presence of litter (with and without litter) were used as fixed effects. The Gaussian distribution was assumed for the response variable and the identity function for the relationship between the response and explanatory variables.

In the greenhouse, the differences in soil type and effect of litter in the emergence percentage and emergence rate were tested using a factorial ANOVA, followed by a post hoc Tukey's test ($p < 0.05$). Before performing ANOVA, data were analyzed for normality using the Kolmogorov–Smirnov test and for homogeneity of variance using the Levene's test. For data that did not show normality and/or variance homogeneity, emergence percentage was arcsine $\sqrt{}$ transformed and germination rate transformed to log(x + 1) (Zar 1999).

All statistical analyses were done with R version 3.0.3 (R Development Core Team 2014), using the 'lme4′ package for GLMM and GLM, 'survival' package for survival analysis and'stats' for Mann–Whitney U test. Figures were performed with R and Origin (version 8.0, OriginLab, MA, Cary, NC, USA).

Results

Seed dispersal

Seed dispersal of *C. equisetifolia* occurred year-round, with the highest number of dispersed seeds recorded in February and March. For *C. hilariana*, the highest seed dispersal occurred in December and March, and for *M. obtusifolia* most seed dispersal took place between January and February (Fig. 1). The average number of *C. equisetifolia* seeds dispersed over a year was higher in the *Casuarina* stand than inside patches ($U < 0.001$; $p < 0.001$). In relation to the native species, the average number of *C. hilariana* dispersed seeds was higher inside patches ($U = 35$, $p = 0.03$), but for *M. obtusifolia* there was no significant difference in the average number of seeds dispersed between *Casuarina* stand and inside vegetation patches ($U = 65$, $p = 0.71$) (Table 2).

Seedling emergence and establishment

There was no significant difference in seedling emergence between the two vegetation types for the three species (Table 3). There was virtually no seedling emergence (P(Em)) of *C. equisetifolia*; only one seedling emerged in each vegetation type, and these all died after one month (Table 4). For the two native species, the position of seed sowing had a significant effect on emergence, with most seedling emergence occurring for seeds sown below litter, and there was no difference between above- and without-litter treatments (Table 3). For *C. hilariana*, seedling emergence occurred in the *Casuarina* stand only for seeds sown below litter, and inside patches for seeds sown below- and above-litter, but all seedlings died within 24 months. *Maytenus obtusifolia* was the species with the highest emergence (Table 4). The interaction between vegetation and seed sowing position was only significant for emergence of *M. obtusifolia,* for which the highest value was in the *Casuarina* stand below litter (Table 3 and 4). No seedlings emerged from the control seed subplots.

The probability of a seed becoming an established seedling was zero for *C. equisetifolia* and *C. hilariana* in both vegetation types within 2 years. *Maytenus obtusifolia* was the only species for which seedlings survived to 24 months; the values of establishment proportion (P(Es)) ranged between 0.02 (±0.04) and 1.00 (±0.00) (Table 4). There was no effect of the vegetation type and litter on the establishment of *M. obtusifolia* seedlings (Table 3).

Emerged seedling represented 0.3 % of recorded seed dispersal for *C. equisetifolia* in both the

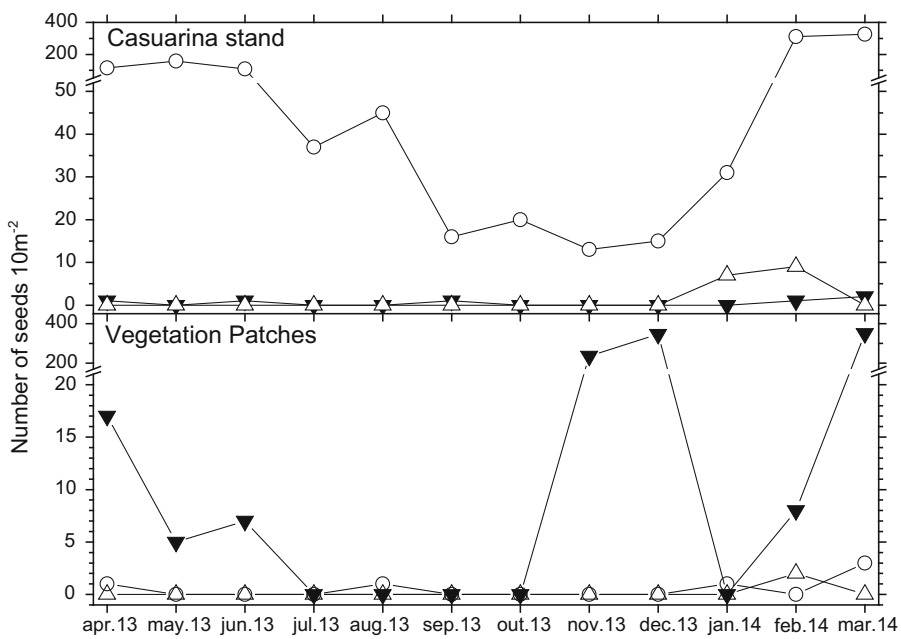

Fig. 1 Total number of seeds dispersed over one year (April 2013 to March 2014) of *Casuarina equisetifolia* (*opened circle*), *Clusia hilariana* (*inverted filled triangle*) and *Maytenus obtusifolia* (*opened triangle*) under the *Casuarina* stand (*upper*) and vegetation patches (*lower*), in the restinga of the Costa do Sol State Park (Brazil). Note the y-axis break in both graphs

Table 2 Mean (±S.D.) number of seeds dispersed of *Casuarina equisetifolia, Clusia hilariana* and *Maytenus obtusifolia* over one year (May 2013 to April 2014), under the *Casuarina* stand and vegetation patches in the restinga of the Costa do Sol State Park (Brazil)

Species	Seeds m^{-2} $year^{-1}$			
	Casuarina stand	Patches	*U*	*p*
C. equisetifolia	199.50 ± 225.06 a	1.0 ± 1.81 b	<0.001	**<0.001**
C. hilariana	1.0 ± 1.35 b	161.67 ± 283.10 a	35	**0.03**
M. obtusifolia	2.67 ± 6.28 a	0.33 ± 1.15 a	65	0.71

In bold are significant values (Mann–Whitney U test; $p < 0.05$)

Different letters indicate significant differences between number of seeds dispersed. Mann–Whitney U test ($p < 0.05$)

Table 3 Statistics for fixed effects of generalized linear mixed model for seedling emergence (after 4 months of seed sowing) and establishment (after 24 months of seed sowing) in relation to vegetation types (*Casuarina* stand and vegetation patches) and seed sowing position (above-litter, below-litter and without-litter) in the restinga of the Costa do Sol State Park (Brazil)

Variable	Estimate	SE	*Z* value	*P*
Casuarina equisetifolia (emergence)				
Intercept	−6.39	1.23	−5.216	**<0.001**
Vegetation patches	1.67 e^{-12}	1.42	0.000	1.000
Below-litter	−2.00 e^{+1}	1.34 e^{+4}	−0.001	0.999
Without-litter	4.84 e^{-15}	1.42	0.000	1.000
Clusia hilariana (emergence)				
Intercept	−4.24	0.56	−7.514	**<0.001**
Vegetation patches	−2.78	1.64	−1.700	0.089
Below-litter	1.44	0.39	3.722	**<0.001**
Without-litter	−20.87	6722.16	−0.003	0.997
Maytenus obtusifolia (emergence)				
Intercept	−5.57	0.90	−6.192	**<0.001**
Vegetation patches	2.27	1.37	1.658	0.097
Below-litter	4.91	0.73	6.736	**<0.001**
Without-litter	0.41	0.92	0.447	0.655
Vegetation patches × below-litter	−4.37	0.77	−5.639	**<0.001**
Vegetation patches × without-litter	0.19	0.96	0.196	0.844
Maytenus obtusifolia (establishment)				
Intercept	0.21	0.62	0.335	0.737
Vegetation patches	−1.05	0.63	−1.655	0.098
Below-litter	−0.39	0.53	−0.751	0.453
Without-litter	0.92	0.54	1.72	0.085

In bold are significant values ($p < 0.05$)

Casuarina stand above litter and inside vegetation patches without litter (Fig. 2). Irrespective of the number of seeds present in the seedfall, seedling emergence was low and at the end of the recruitment process no seedlings of *C. hilariana* survived in either vegetation type (Fig. 2). For *M. obtusifolia,* seedling establishment represented 14.4 % of dispersed seeds in the *Casuarina* stand below litter, inside vegetation patches establishment was 4.2 % of dispersed seeds (Fig. 2).

Young plant survival and growth

The highest survival probability of young plants of *C. equisetifolia* was in the *Casuarina* stand. All plants died inside patches and open area in less than 13 months (Fig. 3a). The risk of *C. equisetifolia* death inside patches was 32 times and in open area 30 times higher than in the *Casuarina* stand (Hazard Ratio (HR) 32.31, Wald's *p* value <0.001; HR 30.37, Wald's *p* value <0.001, respectively). There was no

Table 4 Mean (± S.D) emergence (Em—after 4 months of sowing) and establishment (Es—after 24 months of sowing) proportion of *Casuarina equisetifolia, Clusia hilariana* and *Maytenus obtusifolia* seedlings under *Casuarina* stand and inside vegetation patches, in the restinga of the Costa do Sol State Park (Brazil)

	C. equisetifolia	*C. hilariana*	*M. obtusifolia*
P(Em): Seedling emergence proportion			
Casuarina stand above litter	0.003 ± 0.008	0	0.007 ± 0.010
Casuarina stand below litter	0	0.10 ± 0.09	0.39 ± 0.26
Casuarina stand without litter	0	0	0.01 ± 0.01
Patchy above litter	0	0.03 ± 0.07	0.11 ± 0.17
Patchy below litter	0	0.02 ± 0.03	0.16 ± 0.19
Patchy without litter	0.003 ± 0.008	0	0.17 ± 0.24
P(Es): Seedling establishment proportion			
Casuarina stand above litter	0	0	1.00 ± 0.00
Casuarina stand below litter	0	0	0.37 ± 0.16
Casuarina stand without litter	0	0	0.67 ± 0.01
Patchy above litter	0	0	0.31 ± 0.13
Patchy below litter	0	0	0.20 ± 0.04
Patchy without litter	0	0	0.35 ± 0.18

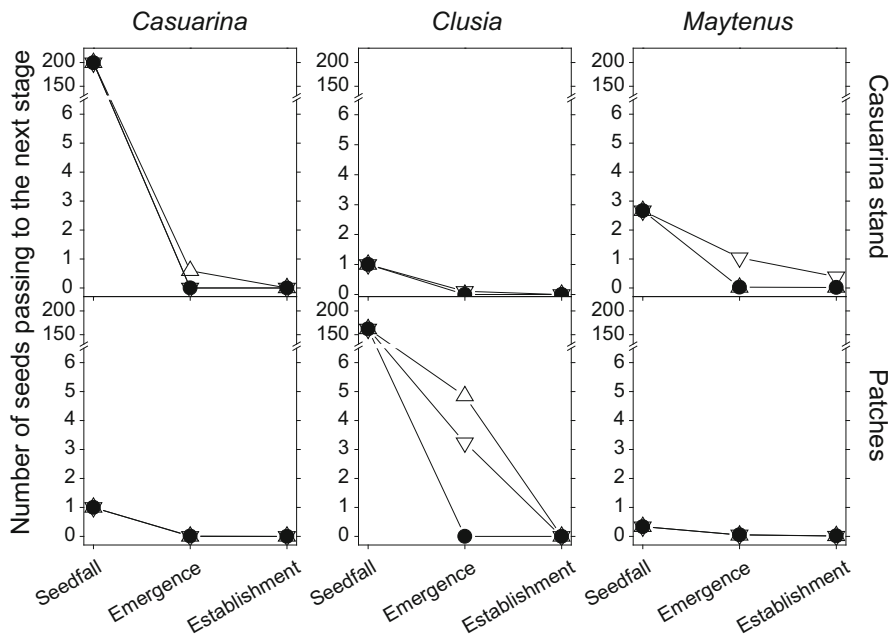

Fig. 2 Recruitment expectancies (m^{-2}) for seedlings of *Casuarina equisetifolia*, *Clusia hilariana* and *Maytenus obtusifolia* under the *Casuarina* stand (*upper*) and vegetation patches (*lower*), in the restinga of the Costa do Sol State Park (Brazil). Seed sowing above litter (*triangle*), below litter (*inverted triangle*) and without litter (*closed circle*). Reproductive stage: Mean seedfall over 1 year (April 2013 to March 2014); Mean cumulative seedling emergence after 4 months of sowing (July 2014); Mean Seedling establishment after 24 months of sowing (February 2016). Proportion of seedling emergence and establishment (Table 3) adjusting for the number of seeds dispersed (Table 2). Note the y-axis break in the graphs

significant influence of litter in the survival of *C. equisetifolia* (HR 1.44, Wald's p value = 0.23).

The probability of survival of young plants of *C. hilariana* was significantly lower in the *Casuarina* stand without litter than under other conditions (Fig. 3b). There was no significant difference between survival rates of *C. hilariana* in relation to the vegetation type (HR 0.28 Wald's p value = 0.60). Litter layer had no significant influence on *C. hilariana* survival inside patches (HR 1.78, Wald's

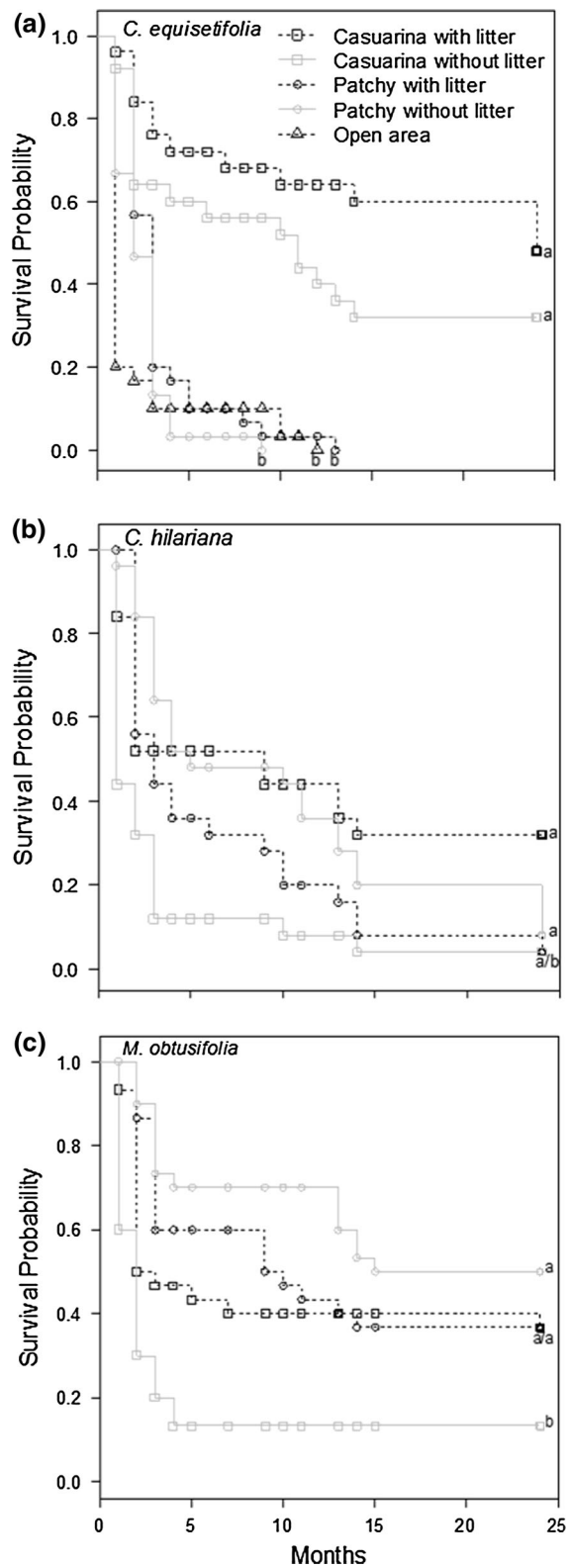

Fig. 3 Survival probability for young plants of *Casuarina equisetifolia* (**a**), *Clusia hilariana* (**b**) and *Maytenus obtusifolia* (**c**) transplanted to *Casuarina* stand with litter and without litter, vegetation patches with litter and without litter and open area (*C. equisetifolia*) in the restinga of the Costa do Sol State Park (Brazil). Monthly evaluations during 24 months (January 2014 until December 2015). Survival analysis was performed with the Kaplan–Meier product limit method. The *letter codes* indicate homogeneous groups (Log-rank test, $p < 0.05$)

p value = 0.18), but the probability of death was almost seven times higher without litter than with litter in the *Casuarina* stand (HR 6.86, Wald's p value = 0.009).

Likewise, the lowest survival rate of young plants of *M. obtusifolia* occurred in the *Casuarina* stand without litter (Fig. 3c). The risk of *M. obtusifolia* death was ten times higher in the *Casuarina* stand than in patches (HR 10.1, Wald's p value = 0.001). There was no significant difference on survival rates in relation to the presence of litter inside patches (HR 1.31, Wald's p value = 0.25). However, in the *Casuarina* stand the probability of death of *M. obtusifolia* without litter was five times higher than with the presence of litter layer (HR 5.32, Wald's p value = 0.02).

After 24 months in the *Casuarina* stand, the highest survival probability was for *C. equisetifolia* (42 %). There was no significant difference between survival rates of the two native species (18.0 % for *C. hilariana* and 25 % for *M. obtusifolia*; Figure S2a). The risk of death in the *Casuarina* stand was almost 13 times higher without litter than with litter (HR 12.71, Wald's p value <0.001) after 24 months (Figure S2b). On the other hand, after 24 months inside vegetation patches, *M. obtusifolia* was the species with the highest probability of survival (43.3 %), followed by *C. hilariana* (6.0 %); there was zero survival for *C. equisetifolia* (Figure S2c). There was no significant difference between survival rates with and without a litter layer (HR 1.43, Wald's p value = 0.23) after 24 months inside patches (Figure S2d). In total, after two years, 34.2 % of young plants of *M. obtusifolia* remained alive. For *C. hilariana* and *C. equisetifolia*, only 12.0 and 19.1 % of young plants survived, respectively. The overall survival rate after 24 months in the *Casuarina* stand was 25.2 and 17.5 % inside patches.

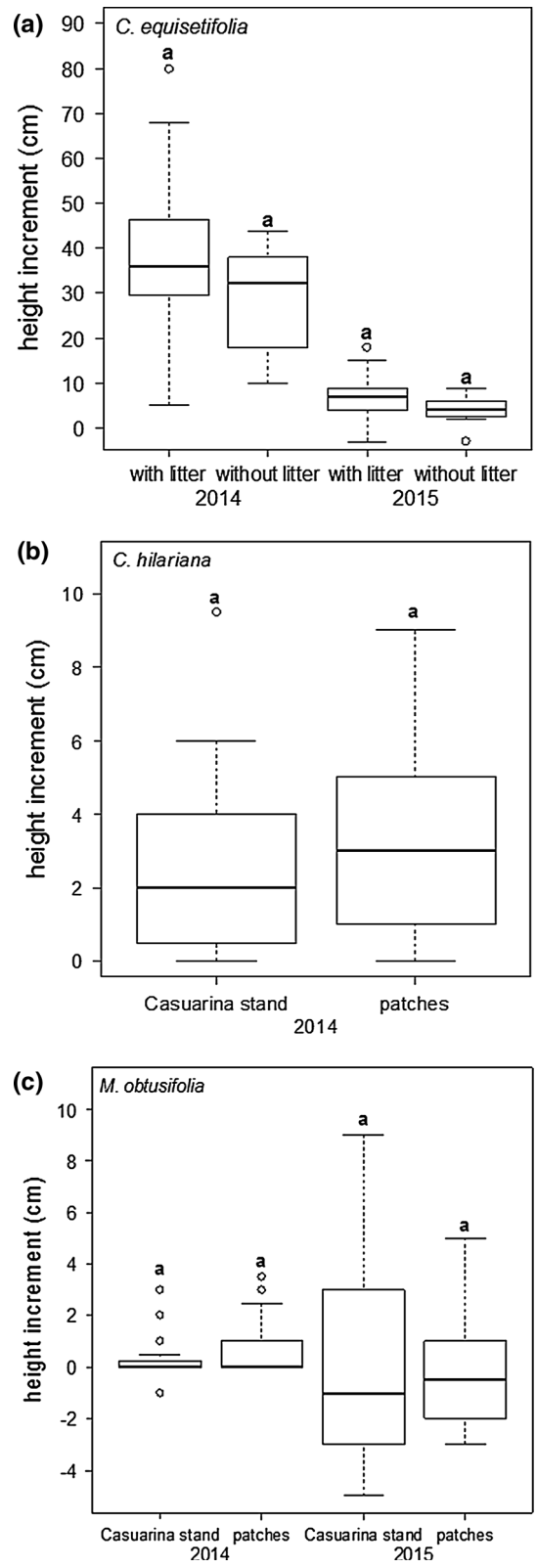

Fig. 4 Height increment for young plants of *Casuarina equisetifolia* transplanted to *Casuarina* stand (**a**), and *Clusia hilariana* (**b**) and *Maytenus obtusifolia* (**c**) transplanted to *Casuarina* stand and vegetation patches in the first (2014) and in the second (2015) year (except for *C. hilariana*) after planting in the restinga of the Costa do Sol State Park (Brazil). The *letter codes* indicate homogeneous groups (GLM, $p < 0.05$)

As almost all young plants of *C. equisetifolia* died before 12 months inside vegetation patches, growth of this species was recorded only in the *Casuarina* stand, and there was no significant difference between height increment with and without a litter layer in both years (Fig. 4a; Table 5). Growth for C. *hilariana* was recorded only in the first year, because most labeled young plants died in the second year. There was no significant difference in height increment for both native species in the first year and for *M. obtusifolia* in the second year between the *Casuarina* stand and vegetation patches (Fig. 4b, c; Table 5). Litter layer also did not affect growth of native species (Table 5). The increase of the number of leaves was higher under *Casuarina* stand than inside vegetation patches for both native species in the first year, but in the second year there was no significant difference for *M. obtusifolia* (Fig. 5; Table 5).

Greenhouse experiments

There was no significant variation in percentage emergence for the three species in relation to soil type. However, emergence rate was significantly higher in soil from patches than in soil collected from the *Casuarina* stand (for both sterilized and non-sterilized treatments), except for *C. hilariana*. The highest moisture content was also in soil from patches (Table 6).

Seedling emergence of *C. equisetifolia* was influenced by the seed sowing position in the litter, with the highest emergence in the control. Emergence percentage and emergence rate was significantly lower below plastic fibers than below litter layer. For *C. hilariana* and *M. obtusifolia* the presence and type of litter layer had no significant effect on the emergence percentage. Litter significantly reduced emergence rate compared to the control treatment, and *Casuarina* litter and plastic fibers had similar effects for the two native species. No seedlings emerged from the seeds

Table 5 Statistics for fixed effects of generalized linear model for young plants growth of *Casuarina equisetifolia* transplanted to *Casuarina* stand, and *Clusia hilariana* and *Maytenus obtusifolia* transplanted to *Casuarina* stand and vegetation patches in the first (2014) and in the second (2015) year (except *C. hilariana*) after planting in the restinga of the Costa do Sol State Park (Brazil)

Variable	Estim.	SE	t value	*p*
Height increment				
Casuarina equisetifolia (Casuarina stand)				
Year 1 (2014)				
Intercept	3.67	0.10	36.18	**<0.001**
Without-litter	−0.29	0.19	−1.45	0.16
Year 2 (2015)				
Intercept	6.85	1.48	4.62	**<0.001**
Without-litter	−2.99	2.51	−1.19	0.25
Clusia hilariana				
Year 1 (2014)				
Intercept	0.86	0.28	3.09	**0.005**
Patch	−0.24	1.31	−0.18	0.85
Without-litter	1.73	1.33	1.30	0.20
Maytenus obtusifolia				
Year 1 (2014)				
Intercept	0.40	0.28	1.40	0.16
Patch	0.54	0.35	1.55	0.13
Without-litter	−0.48	0.33	−1.46	0.15
Year 2 (2015)				
Intercept	−0.14	0.80	−0.17	0.86
Patch	−0.49	0.97	−0.51	0.61
Without-litter	0.61	0.93	0.66	0.52
Increase of the number of leaves				
Clusia hilariana				
Year 1 (2014)				
Intercept	−2.29	1.13	−2.03	0.06
Patch	−6.69	1.84	−2.55	**0.02**
Without-litter	1.85	1.86	0.99	0.33
Maytenus obtusifolia				
Year 1 (2014)				
Intercept	3.41	1.59	2.15	**0.03**
Patch	−6.75	1.94	−3.48	**0.001**
Without-litter	0.12	1.81	0.07	0.95
Year 2 (2015)				
Intercept	1.02	1.35	0.76	0.45
Patch	−2.04	1.62	−1.26	0.22
Without-litter	3.18	1.56	2.04	0.06

In bold are significant values ($p < 0.05$)

of the two native species sown above litter. The moisture content in the control treatment was lower than in the two types of litter. There was no significant difference in moisture content between *C. equisetifolia* litter and plastic fibers (Table 6).

Discussion

Although the restinga has been exposed to propagule pressure from *C. equisetifolia*, seed dispersal of this species into this ecosystem is rare, and there was hardly any seedling emergence and no survival of young plants. While the species is highly invasive in many coastal areas around the world (Rejmánek and Richardson 2013; Potgieter et al. 2014), results of this study suggest that preserved fragments of restinga can resist invasion of this alien tree. In ecosystems characterized by multiple stressful conditions, abiotic barriers are the main factors limiting invasion (Zefferman et al. 2015). In relation to the re-colonization of native species, light availability and soil type are not the main factors responsible for low regeneration in the *Casuarina* stand. Litter appears to be the major factor to prevents seedling emergence. Nevertheless, once plants are established, litter increases the survival of young plants and improves the recovery of native species in the invaded stand (Fig. 6).

Seed dispersal may limit invasion and increase native re-colonization

Restinga sites experience strong winds (Barbiére 1984) and throughout the study period wind speeds of 80.2 km hr^{-1} were recorded (May/2013; INMET 2014) in the restinga of PECSol. Therefore, we expected more *C. equisetifolia* seeds to be dispersed over greater distances than were measured in this study. Many alien tree species with seeds adapted for dispersal by wind frequently spread over hundreds of meters or even kilometers (e.g. *Pinus* species; Richardson and Higgins 1998). Despite apparent adaptations for long-distance dispersal by wind (small seed size and membranous samaras), only 0.5 % of the total *C. equisetifolia* seeds were dispersed between 50 and 100 meters from the edge of the *Casuarina* stand. A similar pattern was reported for dispersal of the

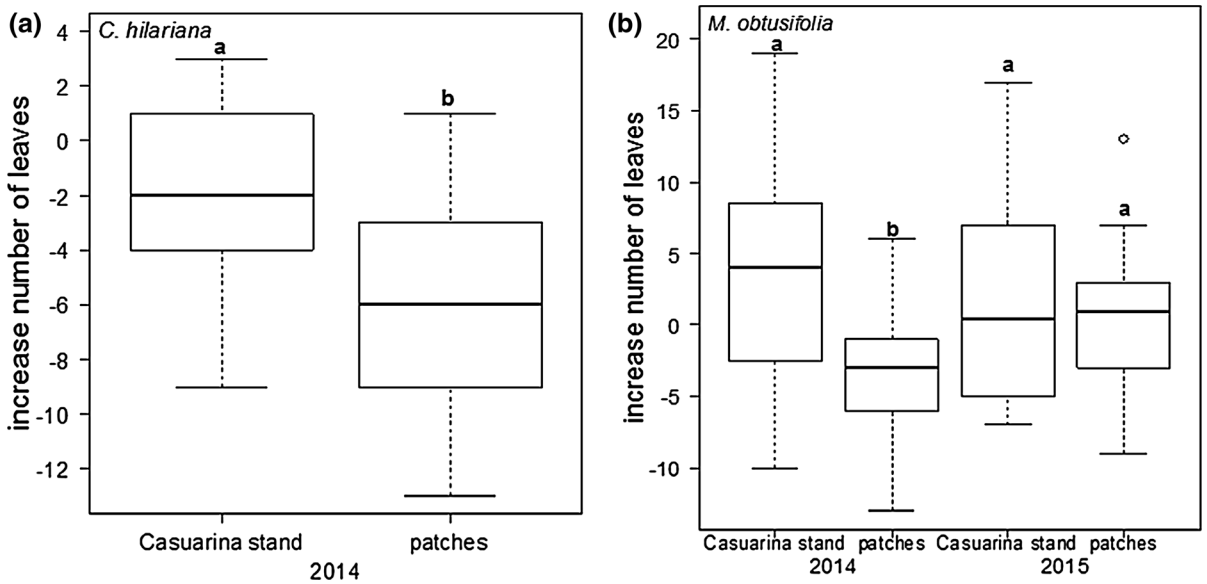

Fig. 5 Increase number of leaves for young plants of *Clusia hilariana* (**a**) and *Maytenus obtusifolia* (**b**) transplanted to *Casuarina* stand and vegetation patches in the first (2014) and in the second (2015) year (except for *C. hilariana*) after planting in the restinga of the Costa do Sol State Park (Brazil). The *letter codes* indicate homogeneous groups (GLM, $p < 0.05$)

wind-dispersed invasive tree *Pinus elliottii* in the restinga; 98 % of the seeds of the pine were dispersed inside or at the edge of the pine stand, with only 2 % moving 30 m beyond the pine stand (Bechara et al. 2013). Thus, although strong winds occur frequently in the restinga, long-distance seed dispersal of *C. equisetifolia* into this ecosystem does not appear to pose a major problem for conservation of this vegetation type (although further research on the dispersal dynamics of *C. equisetifolia* is justified). Seed dispersal by birds appears to be more effective in the restinga, in which seeds of zoochorous native species were dispersed to the *Casuarina* stand—for *M. obtusifolia* in the same quantity as in the restinga. *Casuarina equisetifolia* trees can act as perches, increasing the dispersal rate of native species dispersed by birds and potentially favoring colonization of native species in invaded areas.

Litter can limit or increase seedling emergence and establishment in invaded stands

Although for *C. equisetifolia* the number of emerged seedlings as a proportion of the number of dispersed seeds was similar in the *Casuarina* stand and in vegetation patches, the causes of the low emergence and null establishment in the two vegetation types should be different. The fact that emergence was almost nil under canopies of *Casuarina* trees in the field and in the greenhouse with the presence of litter (above or below) strongly suggests that *Casuarina* litter may be the main barrier limiting its own species recruitment in the *Casuarina* stand. In the restinga, the absence of seedlings in sown patches and in open areas could reflect the lack of suitable germination microsites. As *C. equisetifolia* is intolerant of shade, and since water stress limits germination of its seeds (Zimmermann et al. 2016), shade inside vegetation patches and dry conditions in open areas may be the main ecological mechanisms impeding its invasion in the restinga. Abiotic resistance is therefore the main factor thwarting invasion of *C. equisetifolia* in this ecosystem. Nonetheless, its seeds have the potential to remain viable for approximately 50 months in the soil (Zimmermann et al. 2016), and thus have the capacity to germinate whenever environmental conditions are favorable for germination (Baskin and Baskin 2014), allowing it to colonize new habitats.

Clusia hilariana is an important species contributing to seed dispersal of the restinga. However, like *C. equisetifolia*, it did not recruit in the two vegetation types. In the restinga, the infrequent establishment of *C. hilariana* (Dias et al. 2005) occurs mainly inside the tank of soil bromeliads in vegetation patches (Zaluar

Table 6 Effect of soil type and litter layer on emergence percentage and emergence rate (Mean ± S.D.) of *Casuarina equisetifolia*, *Clusia hilariana* and *Maytenus obtusifolia* in a greenhouse experiment

Species	Soil/Litter	% Emergence	*F*	*p*	Emergence rate (per day 10^{-2})	*F*	*p*	Moisture content	*F*	*p*
Soil										
C. equisetifolia	*Casuarina*	45.20 ± 3.35 a	7.92	0.35	4.36 ± 0.62 b	43.00	**<0.001**	4.65 ± 2.09 b	143.78	**<0.001**
	Sterilized *Casuarina*	48.40 ± 10.81 a			4.73 ± 0.26 b			4.18 ± 1.72 b		
	Patches	54.00 ± 9.38 a			6.60 ± 0.22 a			7.15 ± 2.57 a		
C. hilariana	*Casuarina*	80.00 ± 5.22 a	1.40	0.28	7.97 ± 1.28 a	0.51	0.61	4.92 ± 2.41 b	74.04	**<0.001**
	Sterilized *Casuarina*	72.80 ± 9.55 a			7.18 ± 1.03 a			4.58 ± 2.24 b		
	Patches	78.00 ± 7.42 a			7.70 ± 1.40 a			9.23 ± 2.81 a		
M. obtusifolia	*Casuarina*	50.00 ± 7.86 a	2.89	0.09	2.70 ± 0.16 b	8.45	**0.005**	3.68 ± 1.94 b	94.25	**<0.001**
	Sterilized *Casuarina*	52.22 ± 6.33 a			2.85 ± 0.32 b			3.10 ± 1.63 b		
	Patches	61.11 ± 8.78 a			3.87 ± 0.77 a			7.81 ± 2.46 a		
Litter										
C. equisetifolia	Control	49.60 ± 8.76 a	103.36	**<0.001**	5.66 ± 0.69 a	110.95	**<0.001**	33.96 ± 9.03 b	89.48	**<0.01**
	Below litter	8.80 ± 5.22 b			2.01 ± 0.90 b			56.59 ± 2.91 a		
	Below plastic fibers	0.80 ± 1.79 c			0.02 ± 0.04 c			53.40 ± 4,22 a		
	Above litter	0.00 ± 0.00 d			0.00 ± 0.00 c					
C. hilariana	Control	75.20 ± 10.35 a	109.68	**<0.001**	6.68 ± 0.28 a	767.99	**<0.001**	35.85 ± 3.43 b	578.64	**<0.01**
	Below litter	76.80 ± 9.55 a			2.61 ± 0.27 b			57.95 ± 2.85 a		
	Below plastic fibers	77.60 ± 8.29 a			2.81 ± 0.21 b			55.22 ± 2.30 a		
	Above litter	0.00 ± 0.00 b			0.00 ± 0.00 c					
M. obtusifolia	Control	62.40 ± 8.29 a	89.42	**<0.001**	3.60 ± 0.36 a	236.48	**<0.001**	22.51 ± 3.85 b	58.54	**<0.001**
	Below litter	55.20 ± 6.57 a			2.20 ± 0.22 b			41.02 ± 5.97 a		
	Below plastic fibers	50.40 ± 8.29 a			2.10 ± 0.09 b			40.74 ± 5.58 a		
	Above litter	0.00 ± 0.00 b			0.00 ± 0.00 c					

Mean (±S.D.; $n = 3$) of moisture content for each treatment

In bold are significant values (ANOVA, post hoc Tukey's test; $p < 0.05$)

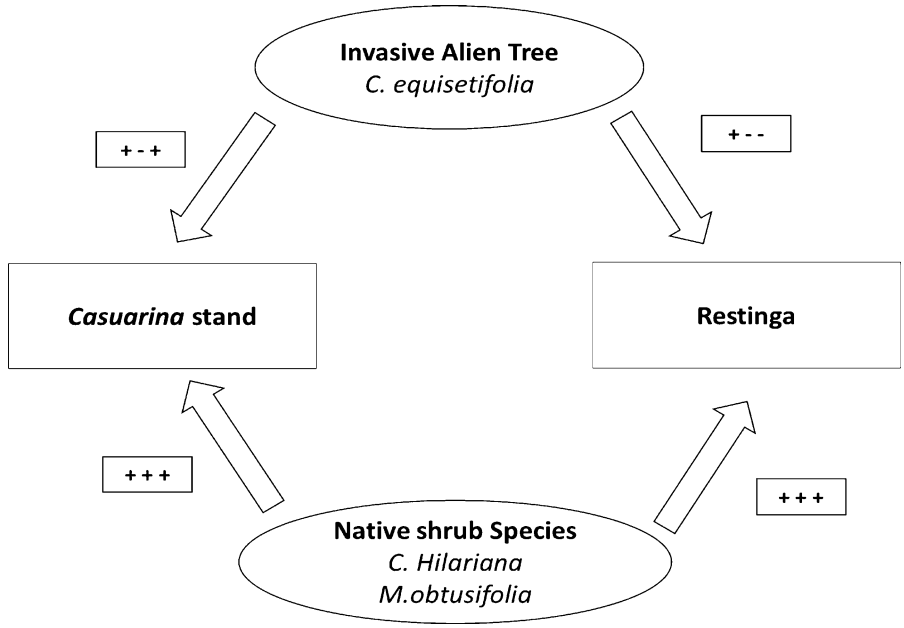

Fig. 6 Interaction model among *Casuarina equisetifolia*, *Clusia hilariana* and *Maytenus obtusifolia* in the *Casuarina* stand and restinga (inside vegetation patches). Positive or negative signs (+, −) indicate possible outcomes for seed dispersal, seedling emergence and young plants survival of the species in each vegetation

and Scarano 2000). The likelihood of a dispersed *M. obtusifolia* seed becoming an established seedling was almost five times higher in the *Casuarina* stand below litter than inside vegetation patches. This helps to drive recolonization of native shrubs in areas invaded by this alien species (Hata et al. 2012). In addition, seedlings of *M. obtusifolia* survived longer than 24 months in both vegetation types, probably due to seedling morphology. Seeds of this species have cotyledon reserves that provide a nutritional supplement to boost embryo growth and seedling survival (Garwwod 1996), thus increasing the likelihood for successful plant establishment in ecosystems with multiple stressful conditions.

Unlike seeds sown below litter, seedling emergence of native species rarely occurred for those sown on top of the litter in the field and in the greenhouse. Litter prevents seed from reaching the soil surface, acting as a physical barrier to dispersing seeds and limiting seedling establishment (West et al. 2014). However, if seeds can penetrate the litter layer they can germinate and seedlings may establish. As there was no differences between levels of seedling emergence below plastic fibers and plant litter in the greenhouse, the negative effect of *C. equisetifolia* litter on seedling emergence must be physical rather than chemical; this agrees with results from other studies (Rotundo and Aguiar 2005; Hovstad and Ohlson 2008). Nevertheless, Nakahira and Ohira (2005) detected allelochemicals in leachates of *C. equisetifolia* litter in bioassay experiments. Further studies are therefore needed to evaluate the response of native species to the allelopathic potential of this alien species.

Differences in light availability between the invaded and preserved restinga had less effect than the presence of litter layer on seedling emergence of native species. This is in contrast to results from a subtropical island, where the difference in the seedling establishment of a native shrub between a *C. equisetifolia* stand and a native forest was explained by the forest type rather than the presence of litter (Hata et al. 2010a). In ecosystems with dry conditions, like the restinga, the litter layer can improve soil moisture, which may increase seedling establishment (Xiong and Nilsson 1999; Warren et al. 2012). This is the main reason why the absence of litter also reduced seedling emergence of native species in the field. Similarly, Hata et al. (2012) observed that removal of litter reduced seedling establishment of a native shrub in an area invaded by *C. equisetifolia*.

As *C. equisetifolia* produces abundant litter with a low decomposition rate and high toxic concentrations of selenium and salts (Parrotta 1993), the release of allelochemicals in the soil of the invaded area as litter decomposed was expected (Wardle et al. 1996). Nevertheless, soil type did not affect the percentage

of seedling emergence; this finding is in line with the results of Hata et al. (2010a) who observed no differences in seedling emergence of a native shrub between soil from a *C. equisetifolia* forest and from a native forest. These results thus strongly suggest that soil in the *Casuarina* stand did not present biochemical compounds that limit plant recruitment. However, soil in the *Casuarina* stand decreased emergence rate in the greenhouse. The highest emergence in soil from patches may be due the high level of soil moisture, which may have accelerated the germination process (Baskin and Baskin 2014).

Litter can improve native plant survival in invaded stands

As for seedlings, no incidence of herbivory was observed and abiotic filters were the main cause of mortality of young plants. Unlike for seedling emergence and establishment, light availability is an important mediator for young plants survival, especially for shade-intolerant species like *C. equisetifolia* (Zimmermann et al. 2016). Although all plants of *C. equisetifolia* died in the restinga, disturbance that increases light availability (i.e. canopy disturbance) mainly near water bodies could improve its survival in this ecosystem and enhance its spread to adjacent vegetation. In the *Casuarina* stand the probability of its survival is high if the species overcome the seedling phase, increasing its population density.

The high canopy cover (1.7 % of light; Matos 2014) should reduce water evaporation inside patches, thus differences in soil water content with presence or absence of litter did not influence survival of young plants in this microsite. Unlike in the *Casuarina* stand, litter improved native plants survival, mainly due the high light conditions in this vegetation (68.5 % light; Zimmermann et al. 2016). Although the CAM photosynthesis (Franco et al. 1996) maximizes water use efficiency, mortality of young plants of *C. hilariana* due to summer drought stress was an important filter for this species. January and February 2015 were very dry months (0.2 and 19 mm, respectively, Figure S1), and may have contributed to the high mortality rate of this native shrub after one year of planting in both vegetation types. *Maytenus obtusifolia* had the highest seedling emergence in the invaded area, however, vegetation patches provide the best conditions for its survival. As *C. hilariana* and *M. obtusifolia* cannot tolerate high light conditions (Matos 2014) and the area invaded by *C. equisetifolia* did not form a closed stand, with some regions under full sunlight conditions, photodestruction may be the main cause of death for both native species.

Litter can be important for survival in the *Casuarina* sand, but did not increase growth of young plants. Although survival of both native plants was low in the invaded area, they grew during the two years, mainly the number of leaves in the first year, which suggests that they may persist and aid in the colonization of the *Casuarina* stand. On the other hand, high survival and relative growth rates of *C. equisetifolia* in the *Casuarina* stand could indicate that the species is competitively superior to native plants, which would allow it to obtain resources more effectively than the slower growing native species (Grotkopp and Rejmánek 2007; Stricker and Stiling 2013). Thus, although native species can colonize the invaded area, the capacity of *C. equisetifolia* to develop monospecific stands could suppress potential re-colonization of the native plants.

Implications for conservation of sandy coastal plains

Although *C. equisetifolia* is an early successional species, with many traits of successful invasive trees, such as rapid-growth, short juvenile period, small seeds and high seed production (Rejmánek and Richardson 1996; Richardson 2006), our study suggests that the spread of this alien species into the preserved restinga is strongly limited by abiotic barriers. As the tree is sensitive to both drought and shade, this resistance is mainly attributable to the scarcity of key resources in this ecosystem, especially low light inside vegetation patches and water stress in open areas. Nevertheless, anthropogenic disturbances are increasing opportunities for invasion by altering the key processes that naturally make the restinga resistant to invasion. Canopy disturbance in areas close to water bodies would therefore decrease resistance to tree invasion at sites where seed dispersal is not limiting, opening the door to negative impacts on the regional biodiversity. Thus, one of the best ways of hampering invasion of *C. equisetifolia* in the restinga is to conserve the remaining fragments.

Light conditions and soil type do not appear to create major barriers to the recruitment of native plant

in the *Casuarina* stand. Accumulation of large amounts of litter is one of the main causes of low establishment in the invaded area; this affects successional pathways on sandy coastal plains. As removal of *C. equisetifolia* is difficult because it has capacity for vegetative regrowth (Morton 1980) and long-term seed persistence in the soil (Zimmermann et al. 2016), other options need to be explored to aid native species recovery in invaded areas. One option is to manage these "novel ecosystems" to enhance the persistence and regeneration of native plant species. A key intervention towards achieving such an aim should involve sowing seeds below litter and planting young plants of native shrubs with litter. Knowledge of the mechanisms that mediate persistence and re-colonization of native species, as detailed in this study, is crucial elements for effective management of the invaded stands.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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